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# Orientation specificity of learning vernier discriminations

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ABSTRACT

Orientation selective neurons in the primary visual cortex typically respond to a range of orientations that covers 20° or more, while in psychophysical experiments, orientation bandwidth is often clearly narrower. Here, we measure the orientation specificity of perceptual learning for vernier discriminations. More than 70 observers, in separate groups, practiced a vernier discrimination task with a constant stimulus orientation. After a 1 h session of training, the vernier was rotated by 2°, 4°, 10°, 20°, 45° or 90°. Improvement through training in the first session transferred to the second session (tested on the next day) up to 10° of stimulus rotation. We found no transfer for rotations of 20°, 45° and 90° Hence, the orientation half-bandwidth of perceptual learning is around 15°, leading to a bandwidth of 30° and corresponding to that of single neurons in early visual cortices, while being narrower than that in higher cortical areas.



## 1. Introduction

Performance in a large number of tasks improves through perceptual learning, e.g. in motion perception (Ball & Sekuler, 1987), texture and pattern discrimination (Fine & Jacobs, 2000; Karni & Sagi, 1991), contrast detection (Sowden, Rose, & Davies, 2002), and visual preference (Rentschler, Jüttner, Unzicker, & Landis, 1999). Several straight forward (and not mutually exclusive) possibilities come to mind to explain this improvement (cf. Gilbert, Sigman, & Crist, 2001). First, increasing the number of neurons reacting to a given stimulus ('recruitment') can improve performance by increasing the signal to noise ratio (e.g. Dinse, Ragert, Pleger, Schwenkreis, & Tegenthoff, 2003; Merzenich et al., 1987). Alternatively, the tuning of neurons can be sharpened, increasing the sensitivity of the neuron for a given stimulus change (e.g. Schoups, Vogels, Quian, & Orban, 2001; Yang & Maunsell, 2004; Fig. 1a and b). In the latter case, the number of neurons activated by one stimulus would actually decrease rather than increase unlike in recruitment (Barlow & Földiák, 1989; Logothetis, Pauls, & Poggio, 1995). A third possibility relies on an enhanced temporal coherence of stimulus responses of individual neurons, and further possibilities are imaginable.

In any of these cases, only a subpopulation of neurons is trained and hence their tuning is changed. Receptive fields of simple and complex cells in the primary visual cortex have a preferred orientation with stimuli presented at non-optimal orientations eliciting far smaller responses than those of the preferred orientation. If one set of these sets of neurons would change its characteristics as a result of training, the improvement achieved through training should disappear after sufficient stimulus rotation, since the 'trained' neurons would no longer be stimulated by the stimulus (Fig. 1a and b). Rotating the stimulus may be considered as the equivalent – in terms of orientation – to shifting the stimulus laterally, out of the receptive fields trained (Fig. 1c). We tested the specificity of improvement in the orientation domain, i.e. how much stimulus rotation is required to remove the amelioration acquired through training for a given stimulus *orientation*, and compared this bandwidth with the orientation bandwidth of other perceptual skills as well as with that of single neurons as reported in the literature.

A number of studies have addressed the orientation bandwidth of orientation sensitive mechanisms in humans, i.e. the amount of stimulus rotation leading to a reduction of the stimulus effect to half its size at the preferred orientation (Blakemore & Nachmias, 1971; Campbell & Kulikowski, 1966; Fahle, 1998; Kulikowski, 1972; Kulikowski, Abadi, & King-Smith, 1973; Movshon & Blakemore, 1973; Notman, Sowden, & Ozgen, 2005; Phillips & Wilson, 1984; Snowden, 1992). Three of these studies used a masking paradigm with grating stimuli (Campbell & Kulikowski, 1966; Kulikowski, 1972; Phillips & Wilson, 1984). In contrast, Blakemore and Nachmias (1971) as well as Movshon and Blakemore (1973) employed after-effects, while Kulikowski et al. (1973) used subthreshold summation. The results obtained with these studies vary over a wide range, from bandwidths of 6–15° (Fahle, 1998; Movshon & Blakemore, 1973; Notman et al., 2005) to 30–60° (Phillips & Wilson, 1984; cf. also De Valois & DeValois, 1988).

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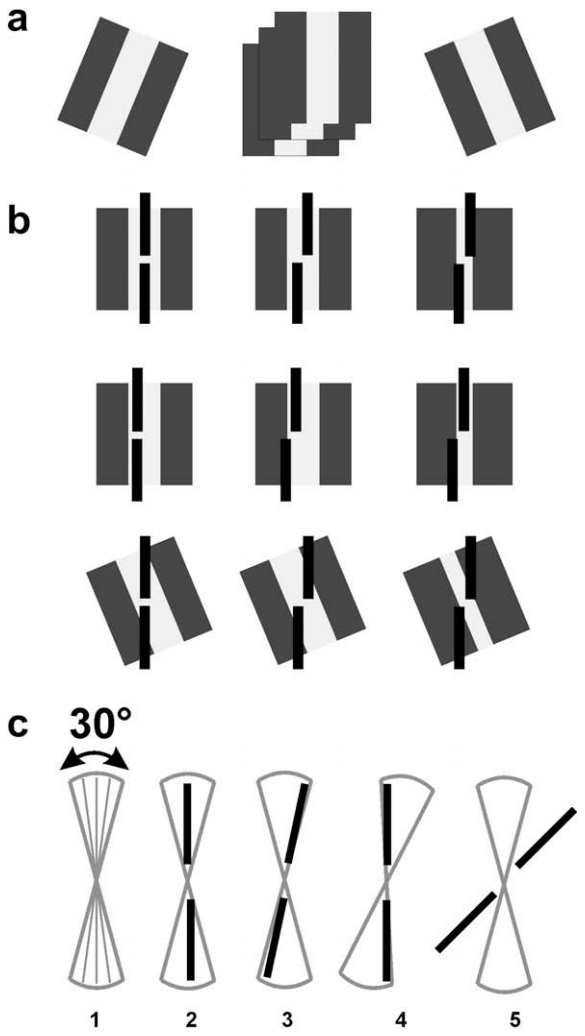


**Fig. 1.** (a) Receptive fields in primary visual cortex usually are organized in a centre-surround antagonism (e.g. excitatory centre with inhibitory side-bands). They cover different positions in the visual field, with differing preferred orientations; (b) learning may decrease the width of the excitatory centre of these neurones, thus sharpening their orientation bandwidth and improving vernier discriminations (after Fahle, 2004). Vernier discrimination by oriented receptive fields. ($c_1$) a receptive field with an orientation bandwidth of 30°; ($c_2$) a vertical vernier within the receptive field of ($c_1$); ($c_3$) rotation of the vernier stimulus by 15° places it at the border of the receptive field; ($c_4$) a neighbouring receptive field with a slightly differing preferred orientation will still react to the vernier stimulus; ($c_5$) a vernier presented at a clearly differing orientation will not activate this neuron.

Improvement in a vernier discrimination task as well as in frequency discrimination does not generalize over rotations of 90° (Fahle & Edelman, 1993; Fahle & Poggio, 2002; Fiorentini & Berardi, 1980) unless for noise-degraded stimuli, (see Fine & Jacobs, 2000) – as to be expected if learning relies on (early) orientation selective filters (Fig. 1a). Perceptual learning of vernier stimuli is moreover specific for the eye used during monocular training (Poggio, Fahle, & Edelman, 1992) and for the exact position in the visual field trained (Fahle, Edelman, & Poggio, 1995). Hence, some forms of perceptual learning seem to involve early visual cortices and one might speculate that learning may indeed improve retinotopically organized early orientation selective mechanisms (Fig. 1a; e.g. Quian & Matthews, 1999; Schiltz et al., 1999; Schoups et al., 2001; Yang & Maunsell, 2004). The present study, as indicated above, compares the orientation bandwidth of perceptual learning with that found on different levels of cortical processing and by different psychophysical paradigms.

## 2. Materials and methods

Vernier stimuli were presented on an X–Y display (Tektronix 608), controlled usually by a PC via fast (>1 MHz pixel rate) custom-made 16 bit D/A converters. Verniers were about 1 arc min wide and 21 arc min high including a vertical gap of 1 arc min at the observation distance of 2 m. Displacement was always perpendicular to the orientation of the vernier segments. Verniers were presented at a refresh rate of 100 Hz with a luminance around 60 cd/m$^2$ as determined by measuring a square area of identical dot density and refresh rate. Background illumination was around 0.5 lux. Stimuli were presented for 150 ms. Observers had to indicate, in a binary forced choice task, whether the lower vernier segment was shifted to the right or to the left relative to the upper segment by pressing the corresponding button. Observer's heads were usually supported by a chinrest and brow-bar.

Before the experiment proper, we determined vernier discrimination thresholds individually for each observer. The verniers were usually oriented horizontally during this pre-test rather than the near vertical or oblique orientations used in the actual experiment. Observers indicated whether the right vernier element was offset up- or downwards compared to the left one. The threshold was determined by fitting a psychometric function based on maximum likelihood analysis and determining the offset size for which 75% correct responses were obtained. For most observers, the threshold calculated corresponded roughly to the last level tested by the staircase procedure. An auditory error signal resounded after incorrect responses and the next presentation followed 0.5 s after the observer's response.

On the basis of the psychometric function, a fixed vernier offset was chosen, expected to yield around 75% correct responses for each individual observer. Observers subsequently trained for 1 h, corresponding to 18 to 20 blocks of 40 presentations each, with verniers rotated by different amounts relative to the vertical. After at least one night's sleep, one additional block with the same orientation was tested, followed by a block testing verniers at a second orientation. This second orientation was mirror-symmetric to the previous one relative to the vertical (with the exception of the stimuli oriented horizontally or vertically) and differed from the first orientation by 2°, 4°, 10°, 20°, 45°, or 90°. For example, in the 2° difference condition, the first orientation was rotated 1° clockwise from the vertical, whereas the second orientation was rotated 1° counter clockwise (or vice versa). Orientations were counterbalanced across subjects. Observers then trained with the second orientation for another 20 blocks. The experiment ended with a retest of the first orientation.

Subjects were mostly students from Tübingen or Bremen University or from high schools. Altogether, 73 paid observers (49 females, aged between 19 and 52 years) participated after the procedure had been fully explained to them. No subject participated in more than one experiment. All observers were naive as to the exact aim of the study and none had previously participated in psychophysical experiments. All had normal or corrected-to-be normal visual acuity. Observers were randomly distributed to one of 6 groups consisting of 12 participants each (except that 19 observers contributed to the 90° condition while only 6 to the 2° condition). In the 90° group 10 subjects saw horizontal and vertical stimuli while nine others saw oblique ones. The data of two observers (one from the 4° group and one from the 10° group) were excluded from the analysis since their results strongly decreased during the first session, making it impossible to test for transfer of (non existing) improvement. All data were transformed from percentages of correct responses to $d'$ in order to account for the non-linear nature of the psychometric function, by applying:

$$d' = \sqrt{2} \times \Phi^{-1}(\mathrm{pc}) \qquad (1)$$

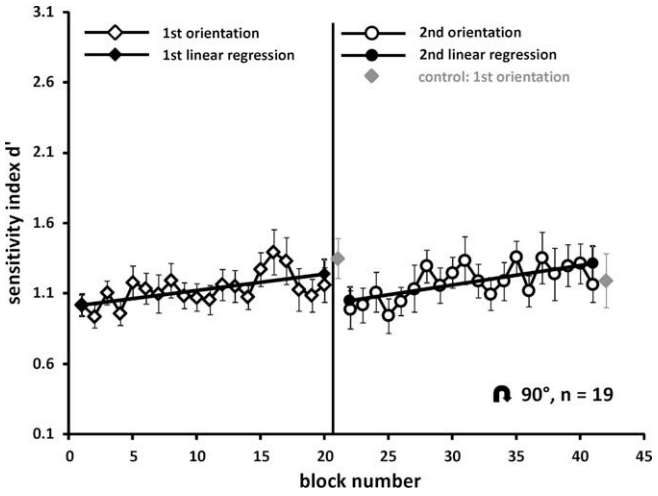


**Fig. 2.** Performance, expressed as the sensitivity index $d'$ calculated on the basis of percentages of correct responses, for 19 observers training a vernier discrimination task. Five observers discriminated, in a first session, between horizontal stimuli, five others between vertical stimuli, and nine others between oblique stimuli. After 20 blocks, corresponding to 1 h of training, stimuli were rotated by 90°. While observers significantly improved performance for both sessions, there was no transfer of improvement between orientations. Each data point represents the mean (±standard error) of 19 observers who each contributed 40 responses per data point in the graphs, leading to 760 responses per data point.

where $\Phi$ is the normal distribution function and (pc) corresponds to percent correct (Macmillan & Creelman, 2005).

To determine improvement of performance in a given session, we fitted regression lines to the individual data of each observer. Results of both sessions of each individual were fitted separately by means of linear regressions on the $d'$ data. A one-sample, one-sided $t$-test indicated whether or not the slopes of the regression lines were significantly higher than zero.

## 3. Results

In the 90° difference condition, five group members started with a horizontal stimulus orientation, five started with a vertical stimulus orientation (constituting the 10 members of group 1) while nine started with an oblique stimulus orientation (group 2). A 3 way ANOVA (session * slope/intercept * group) yielded no significant differences between the results of the two groups, hence their data were combined. Slopes of regression lines through the data of individual observers were on average significantly larger than zero for the first session ($p < 0.01$; Fig. 2). This is to say that performance improved significantly through training. After rotation of the stimuli by 90°, mean performance dropped. Hence training with one orientation of the vernier stimuli seems not to transfer (completely) to the perpendicular stimulus orientation. This impression of absent or incomplete transfer is reflected by the fact that the performance level at the start of the second orientation, as inferred from the regression analysis, did not differ significantly from the level obtained at the start of the first session, i.e. there was no significant improvement from the first stimulus orientation to the second orientation (one-sided paired $t$-test). On the other hand, the performance level attained at the end of the first session, again as inferred from the regression analysis, differed from the level at the start of the second orientation. This trend almost reached significance ($p = 0.051$). Subsequent training, with the second, perpendicular orientation, significantly improved performance (one-sided $t$-test: $p < 0.01$). As we will see below, this is in contrast with the results for those orientation differences yielding transfer of improvement: there, no significant improvement occurred during the second session.

The second experiment tested the transfer of learning for an orientation difference of 45°. Before training, observers obtained on average 69.8% correct responses, corresponding to a $d'$ of 0.77. Training, as measured by the slopes of regression lines through the results of individual observers, significantly improved performance in the first session, for a vernier orientation of 22.5° (counter) clockwise relative to the vertical ($p < 0.05$, one-sided paired $t$-test, to 77.4%, corresponding to $d' = 1.1$; Fig. 3). Rotating the stimulus by 45 to an orientation mirror-symmetric to the vertical abruptly decreased performance. As a consequence, the intercepts of the regression lines of the second session did not differ significantly from those of the first session. Performance improved significantly in the second session ($p < 0.05$), unlike in the experiments yielding transfer between stimulus orientations.

In the third experiment, stimulus orientations differed by 20° between sessions, i.e. the stimulus was first rotated by 10° (counter) clockwise from the vertical while the second orientation was mirror-symmetric to the first one. Initial vernier performance of this group of observers was similar to that of the previous group (Fig. 4). The results again demonstrate a significant improvement through training in both sessions (one-sided $t$-tests: $p < 0.05$ for

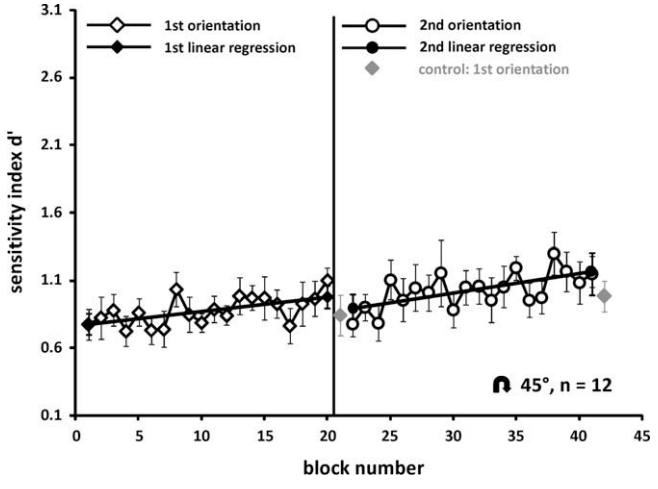


**Fig. 3.** Performance in a vernier discrimination task as a function of training and of stimulus orientation, as in Fig. 2, but difference of stimulus orientation was 45°. Results of 12 observers.

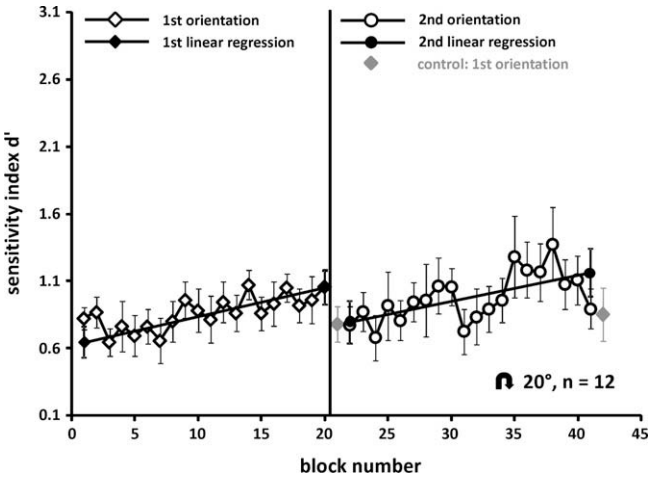


**Fig. 4.** Performance in a vernier discrimination task as in Figs. 2 and 3. Stimulus orientations differed by 20°. Means of 12 observers.

both sessions). Again, the mean intercepts of regression lines through the results of individual observers did not differ significantly between the two sessions, indicating a lack of transfer from the first session to the second. The performance level at the end of the first session, on the other hand, tended to be higher than that at the start of the second session, while this difference failed to reach significance ($p = 0.051$).

The fourth experiment tested transfer of improvement through a change of stimulus orientation of 10° (Fig. 5). The results differ clearly from the ones obtained with the 20° change in stimulus orientation, since observers improved only in the first session ($p < 0.01$), but failed to improve significantly in the second session. Performance did not differ between the first and second session. This lack of improvement in the second session may be caused by transfer of improvement between the two stimulus orientations, as outlined in the discussion. In line with this interpretation, the starting level, or intercept, of the second session was significantly better than the starting level of the first session ($p < 0.05$). Also in line with this interpretation, performance at the end of the first session did not differ significantly from performance at the start of the second session.

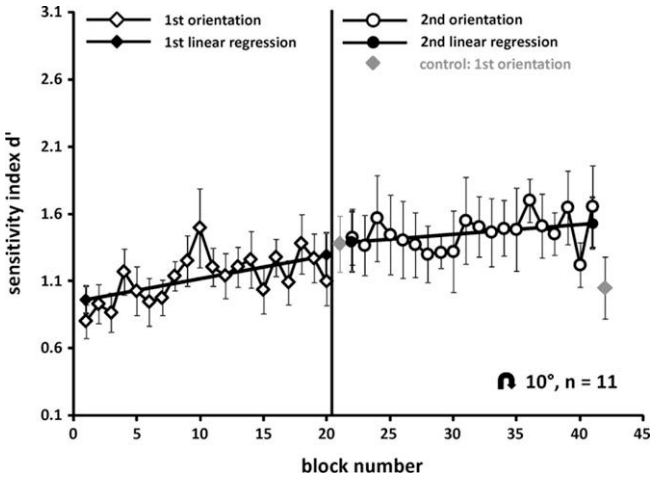


**Fig. 5.** Vernier discrimination as a function of training and orientation, as in Figs. 2–4. Stimulus orientations differed by 10°. Means of 11 observers.

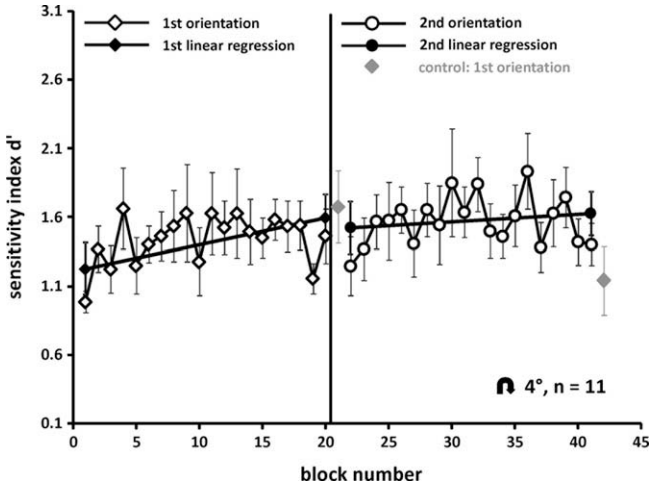


**Fig. 6.** Vernier discrimination as function of training and orientation. Stimulus orientations differed by 4°. Means of 11 observers.

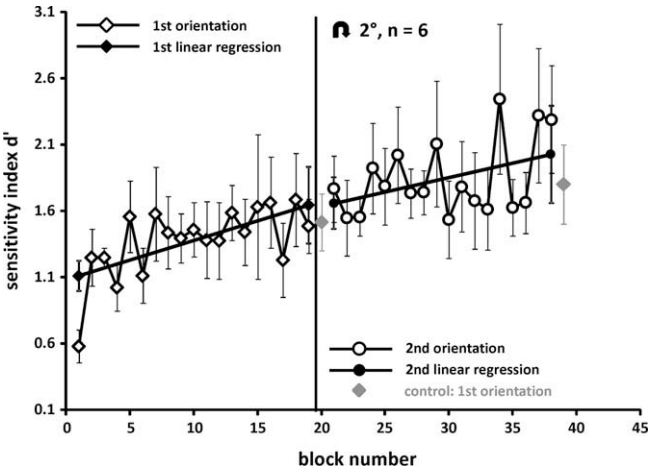


**Fig. 7.** Vernier discrimination as function of training and orientation. Stimulus orientations differed by 2°. Means of six observers.

The fifth group of observers experienced a change of stimulus orientation of 4°. The results are similar to those of the fourth group (see Fig. 6). Observers improved significantly in the first session ($p < 0.05$), but not in the second session. The difference between the starting levels in the first and second session does not reach significance for these observers, but at least shows a trend ($p = 0.085$). The difference between performance at the end of the first session did again not differ from that at the start of the second session, indicating transfer of improvement.

Stimulus orientation changed by only 2° for the last group of observers (Fig. 7). Performance again improved significantly in the first session ($p < 0.05$), while not during the second one. Results from Fig. 7 show that improvement through training seems to transfer completely over such a small orientation change with the second session starting significantly higher than the first one ($p < 0.01$ for the difference between the intercept of session 2 versus the intercept of session 1), and no (significant) drop of performance at the transition between sessions.

## 4. Discussion

A first important result of our study is the high inter-observer and intra-observer variability present in the data (see also Fahle & Henke-Fahle, 1996). The first experiment started with perceptual learning at oblique orientations, i.e. 45°, yielding a far smaller amount of improvement than in the original study by Poggio, Fahle and Edelman (1992). Therefore, after testing nine observers with oblique orientations, we added another 10 subjects using the cardinal orientations as in the earlier study. However, even in the cardinal orientations, improvement was clearly less pronounced in the new tests than in the original study. We conclude that experiments on perceptual learning should, as a rule, test far more observers than used in standard experiments with trained observers, preferably (close to) double-digit numbers for each condition to take into account this high amount of inter-observer variance. However even with the relatively high number of subjects in the present study, we find differences in the speed of improvement between experiments that we would not like to attribute to differences in stimulus conditions but rather to differences in the extend and speed of perceptual learning in different individuals. As a consequence of this variance, the results for the re-testings of the first stimulus condition at the start and end of the second session are, in our opinion, too variable to allow a sound interpretation.

**Table 1**
Summary of statistical results. *n* = Number of subjects; m = male; f = female.

| Orientation difference | *n* | m/f | Improvement in 1st session | Improvement in 2nd session | Difference in starting levels | Drop in performance between sessions |
|---|---|---|---|---|---|---|
| 2° | 6 | 1/5 | $t = 2.7$, $p < .05$ | n.s. | $t = -4.0$, $p < .01$ | n.s. |
| 4° | 11 | 2/9 | $t = 2.1$, $p < .05$ | n.s. | n.s. ($p = .085$) | n.s. |
| 10° | 11 | 4/7 | $t = 2.9$, $p < .01$ | n.s. | $t = -2.2$, $p < .05$ | n.s. |
| 20° | 12 | 5/7 | $t = 2.7$, $p < .05$ | $t = 2.5$, $p < .05$ | n.s. | n.s. ($p = .051$) |
| 45° | 12 | 3/9 | $t = 2.4$, $p < .05$ | $t = 2.1$, $p < .05$ | n.s. | n.s. |
| 90° | 19 | 9/10 | $t = 3.1$, $p < .01$ | $t = 3.4$, $p < .01$ | n.s. | n.s. ($p = .051$) |

The main result, however, is very clear. Vernier discrimination in the first session improved significantly as a result of 1 h of training in all groups of observers. Performance in the second session, on the other hand, improved significantly only in experiments testing orientation differences of more than 10° (see Table 1). This difference of improvement between the first and second session in the experiments testing orientation differences of 10° or less is interpreted as a sign that improvement transferred (more or less completely) between orientations differing by 10° or less. The reason for this interpretation is that perceptual learning is relatively fast at first, slowing down thereafter when performance asymptotically approaches an optimal value. If improvement does not transfer between orientations, perceptual learning starts "from scratch" at the beginning of the second session, and improves significantly during this second session. If, on the other hand, improvement transfers between orientations and hence between sessions, performance starts at a higher level at the beginning of the second session than at the beginning of the first session and hence has less "room" for improvement.

Fig. 8 plots the amount of improvement, i.e. the difference between the starting level for the second orientation (as measured by the intercept of a linear regression) and the starting level of the first session, for all six experiments. The improvement at the start of the second orientation relative to the start of the first session is most pronounced for the smallest changes in orientation and virtually absent for a rotation by 90°. The latter finding corroborates the results of earlier studies (e.g. Poggio et al. 1992). A regression analysis of the data of Fig. 8 ($y = 0.42\, e^{-0,029x}$) yields an $r^2$ of 0.909, indicating a good fit. The results for orientation differences of 2°, 4°, and 10° differ significantly from zero (see Table 1), indicating that improvement transfers between stimulus orientations of 10° and less.

In line with this interpretation, mean performance dropped for all groups after the stimulus was rotated between sessions by more than 10 , but his drop failed to reach significance, if only narrowly so, for two experiments ($p = 0.051$ in both experiments; see Table 1).

We here suppose that in perceptual learning all neurons activated by a stimulus may modify their receptive field properties (or weights at the next level of analysis) if a stimulus falls within their 'window of visibility' and that all neurons influenced by a stimulus contribute to its analysis (for alternative models, cf. Dosher & Lu, 1998; Westheimer, Shimamura, & McKee, 1976). According to this supposition, testing vernier discrimination after a slight stimulus rotation relative to the trained orientation should transfer improvement for two reasons. First, neurons with a preferred orientation corresponding to the *trained* orientation would still be activated quite strongly by a slightly rotated vernier. Second, those neurons with a preferred orientation corresponding to the *rotated* stimulus were rather strongly activated also during the training phase.

The orientation bandwidth of perceptual learning can then be directly inferred from Fig. 8, in analogy to the psychophysical measurements cited in the Introduction. The amount of transfer between the two sessions expressed in terms of $d'$, decreases almost linearly with the log of orientation difference, i.e. the larger the difference between the orientation of the trained stimulus and that of the stimulus tested, the smaller is the transfer of improvement from the first stimulus to the second. While we find full transfer for an orientation difference of 2° (see Fig. 7), corresponding to a difference in starting levels of roughly $d' = 0.55$ (see Fig. 8), transfer at 20° orientation difference is clearly less than half this value ($d' = 0.15$). From these data, we estimate the orientation half-bandwidth to be around 15°, This leads to a bandwidth of around 30° for perceptual learning of vernier discriminations which might be slightly narrower than the *upper limit* found for transfer in complex gratings, where transfer occurs over ±30° rota-

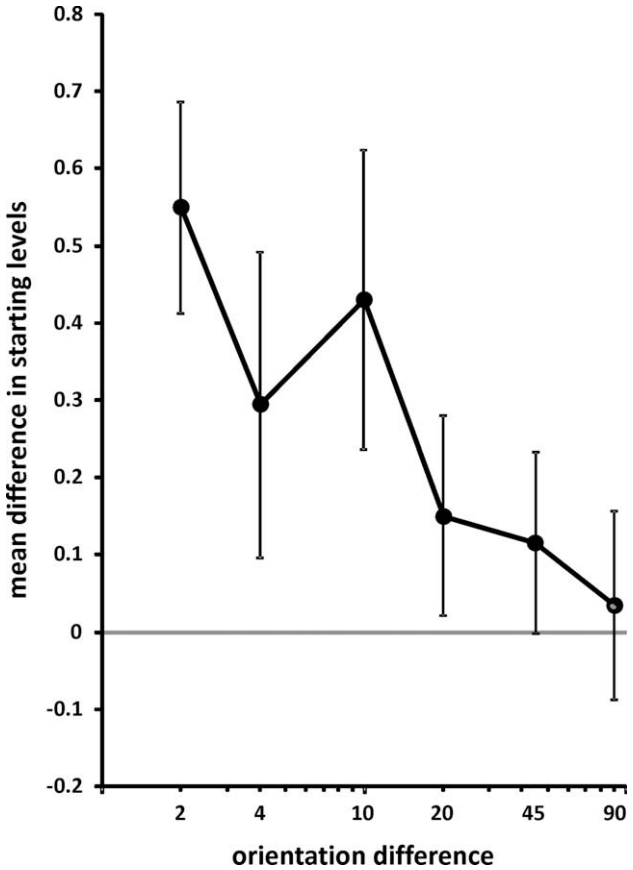


**Fig. 8.** Improvement of performance at the start of the second session expressed as difference in d′, corresponding to the second stimulus orientation, relative to performance at the start of the first session, for all orientation differences tested (orientation differences in deg.).

tion but which is difficult to convert to bandwidth (Fiorentini & Berardi, 1980).

The orientation bandwidth as investigated psychophysically by means of simultaneous masking is around 12–15° for high spatial frequencies (Campbell & Kulikowski, 1966), while wider for lower spatial frequencies (Phillips & Wilson, 1984). The bandwidth is clearly narrower, at around 7° for masking (Kulikowski, 1972), functional magnetic resonance imaging (Mukai et al., 2007) and for orientation selectivity of visual neurons as investigated by single cell recordings (e.g. Movshon, 1979; Ashbridge, Perrett, Oram, & Jellema, 2000). Finally, the bandwidth is as small as around 5° for sub-threshold summation paradigms (Kulikowski et al., 1973) and 10° for adaptation at low luminance levels (Blakemore & Nachmias, 1971; Movshon & Blakemore, 1973). The orientation bandwidth of single cells in early cortical areas (Ashbridge & Perrett, 1998; De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1965; Vidyasagar & Sigüenza, 1985), is roughly in the same range, while clearly wider in intermediate areas such as V4 (around 35°; Yang & Maunsell, 2004) as well as in higher cortical areas such as inferior temporal cortex (IT; Vogels & Orban, 1994b) and anterior inferior temporal cortex (AIT; Tanaka & Fujita, 1991).

Given the wide range of orientation bandwidths communicated in the literature, with orientation bandwidth strongly depending on the type of test applied, it is far from trivial to interpret our results in terms of neuronal mechanisms. However, it is clear that the moderately high orientation specificity apparent in our results is close to the orientation bandwidth usually ascribed to single neurons in the primary visual cortex, and clearly narrower than the wider bandwidth at higher levels of cortical processing.

It seems to be generally agreed that neurons on 'higher' levels of cortical processing abstract from 'mundane' features of stimuli such as their orientation or position in the visual field. Thus, if they achieve this aim, they should certainly be able to transfer the improvement obtained with one class of stimuli to another, similar class – since generalization seems to be their task. The fact that the improvement obtained through training is, in the case of vernier discriminations, rather specific for stimulus orientation, therefore is another argument for plasticity at early stages of cortical processing. Single cell recordings indeed demonstrate plasticity on relatively early cortical levels in primate visual systems (Gilbert et al., 2001; Christ, Li, & Gilbert, 2001; Zohary, Celebrini, Britten, & Newsome, 1994; Vogels & Orban, 1994a, 1994b; Schoups et al., 2001; Schwartz, Maquet, & Frith, 2002; Yang & Maunsell, 2004). Imaging experiments in perceptual learning in addition show a change of activation in primary visual cortex (Mukai et al., 2007; Schiltz et al., 1999; Schwartz et al., 2002; Vaina, Belliveau, Burin de Roziers, & Zeffiro, 1997) in line with earlier sum-potential recordings in humans (Fahle & Skrandies, 1994).

However, the exact neuronal mechanisms underlying perceptual learning in the visual system remain somewhat controversial (Mollon & Danilova, 1996). Of course, perceptual learning may be faster and more easily achieved in "higher" cortical areas. But we continue to conjecture that to achieve optimal results, "late selection" of signals (Fahle, 2004) may not be sufficient, while very early filters must be adapted to the specific task to be solved. This adaptation should not rely primarily on (bottom up) permanent modifications of receptive field widths in early cortical areas or on similar changes leading to a sharpening of orientation discrimination. Such permanent changes in receptive field structure as a result of training one specific task might have unwanted side effects, influencing the processing of *all* types of visual stimuli of the given orientation (e.g. Herzog & Fahle, 1998; Marr, 1982). Hence, we assume a switching of filter specifications in early visual cortices in a task-dependent way under top-down control as the basis of "high end" perceptual learning (Fahle, 2009).

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## References

Ashbridge, E., & Perrett, D. I. (1998). Generalizing across object orientation and size. In V. Kulikowsky & J. Walsh (Eds.), *Perceptual constancy: Why things look as they do*. Cambridge University Press.
Ashbridge, E., Perrett, D. I., Oram, M. W., & Jellema, T. (2000). Effect of image orientation and size on object recognition: Responses of single units in the macaque monkey temporal cortex. *Cognitive Neuropsychology, 17*, 13–34.
Ball, K., & Sekuler, R. (1987). Direction-specific improvement in motion discrimination. *Vision Research, 27*, 953–965.
Barlow, H., & Földiák, P. (1989). Adaptation and decorrelation in the cortex. In R. Durbin (Ed.), *The computing Neuron*. Addison-Wesley.
Blakemore, C., & Nachmias, J. (1971). The orientation specificity of two visual after-effects. *Journal of Physiology (London), 231*, 157–174.
Campbell, F. W., & Kulikowski, J. J. (1966). Orientation selectivity of the human visual system. *Journal of Physiology, 187*, 437–445.
Christ, R. E., Li, W., & Gilbert, C. D. (2001). Learning to see: Experience and attention in primary visual cortex. *Nature Neuroscience, 4*, 519–525.
Dinse, H. R., Ragert, P., Pleger, P., Schwenkreis, P., & Tegenthoff, M. (2003). Pharmacological modulation of perceptual learning and associated cortical reorganisation. *Science, 301*, 91–94.
De Valois, R. L., Yund, E. W., & Hepler, N. (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research, 22*, 531–544.
De Valois, R. L., & DeValois, K. K. (1988). *Spatial vision*. Oxford: Oxford University Press. pp. 264–267.
Dosher, B. A., & Lu, Z. L. (1998). Perceptual learning reflects external noise filtering and internal noise reduction through channel reweighting. *Proceedings of the National Academy of Sciences of the United States of America, 95*, 13988–13993.
Fahle, M. (1998). Orientation specificity of perceptual learning. *Investigative Ophthalmology & Visual Science, 39/4*, 912 (ARVO Abstract).
Fahle, M. (2004). Perceptual learning: A case for early selection. *Journal of Vision, 4*, 879–890.
Fahle, M. (2009). Perceptual learning and sensomotor flexibility: Cortical plasticity under attentional control? *Philosophical Transactions of the Royal Society B, 364*, 313–319. doi:10.1098/rstb.2008.0267.
Fahle, M., & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range, and of feedback. *Vision Research, 33*, 397–412.
Fahle, M., Edelman, S., & Poggio, T. (1995). Fast perceptual learning in hyperacuity. *Vision Research, 35*, 3003–3013.
Fahle, M., & Henke-Fahle, S. (1996). Inter-observer variance in perceptual performance and learning. *Investigative Ophthalmology & Visual Science, 37*, 869–877.
Fahle, M., & Poggio, T. (Eds.). (2002). *Perceptual Learning*. Cambridge, MA: MIT-Press.
Fahle, M., & Skrandies, W. (1994). An electrophysiological correlate of perceptual learning in humans. *German Journal of Ophthalmology, 3*, 427–432.
Fine, I., & Jacobs, R. A. (2000). Perceptual learning for a pattern discrimination task. *Vision Research, 40*, 3209–3230.
Fiorentini, A., & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature, 287*, 43–44.
Gilbert, C. D., Sigman, M., & Crist, R. E. (2001). The neural basis of perceptual learning. *Neuron, 31*, 681697.
Herzog, M. H. H., & Fahle, M. (1998). Modelling perceptual learning: Difficulties and how they can be overcome. *Biological Cybernetics, 78*, 107–117.
Hubel, D. H., & Wiesel, T. N. (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. *Journal of Neurophysiology, 28*, 229–289.
Karni, A., & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Science of the USA, 88*, 4966–4970.
Kulikowski, J. J. (1972). Orientational selectivity of human binocular and monocular vision revealed by simultaneous and successive masking. *Journal of Physiology (London), 226*, 67–68.
Kulikowski, J. J., Abadi, R., & King-Smith, P. E. (1973). Orientational selectivity of grating and line detectors in human vision. *Vision Research, 13*, 1479–1486.
Logothetis, N. K., Pauls, J., & Poggio, T. (1995). Shape representation in the inferior temporal cortex of monkeys. *Current Biology, 5*, 552–563.
Macmillan, N. A., & Creelman, C. D. (2005). *Detection theory: A user's guide (p. 172)*. Mahwah, NJ: Lawrence Erlbaum Associates.
Marr, D. (1982). *Vision*. San Francisco: Freeman & Comp.
Merzenich, M. M., Nelson, R. J., Kaas, J. H., Stryker, M. P., Jenkins, W. M., Zook, J. M., et al. (1987). Variability in hand surface representations in areas 3b and 1 in adult owl and squirrel monkeys. *Journal of Comparative Neurology, 258*, 281–296.
Mollon, J. D., & Danilova, M. V. (1996). Three remarks on perceptual learning. *Spatial Vision, 10*, 51–56.

Movshon, J. A. (1979). *Two-dimensional spatial frequency tuning of cat striate cortical neurons, abstracts, 9th annual meeting* (p. 799). Atlanta, GA: Society for Neuroscience.

Movshon, J. A., & Blakemore, C. (1973). Orientation specificity and spatial selectivity in human vision. *Perception, 2*, 53–60.

Mukai, I., Kim, D., Fukunaga, M., Japee, S., Marrett, S., & Ungerleider, L. G. (2007). Activations in visual and attention-related areas predict and correlate with the degree of perceptual learning. *Journal of Neuroscience, 27*, 11401–11411.

Notman, L. A., Sowden, P. T., & Ozgen, E. (2005). The nature of learned categorical perception effects: A psychophysical approach. *Cognition, 95*, B1–14.

Poggio, T., Fahle, M., & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science, 256*, 1018–1021.

Phillips, G. C., & Wilson, H. R. (1984). Orientation bandwidths of spatial mechanisms measured by masking. *Journal of the Optical Society of America A. Optics and Image Science, 1*, 226–232.

Rentschler, I., Jüttner, M., Unzicker, A., & Landis, T. (1999). Innate and learned components of human visual preference. *Current Biology, 9*, 665–671.

Quian, N., & Matthews, N. (1999). A physiological theory for visual perceptual learning of orientation discrimination. *Society for Neuroscience Abstract, 25*, 1316.

Schiltz, C., Bodart, J. M., Dubois, S., Dejardin, S., Michel, C., Roucoux, A., et al. (1999). Neuronal mechanisms of perceptual learning: Changes in human brain activity with training in orientation discrimination. *Neuroimage, 9*, 46–62.

Schoups, A., Vogels, R., Quian, N., & Orban, G. (2001). Practicing orientation identification improves orientation coding in V1 neurons. *Nature, 412*, 549–553.

Schwartz, S., Maquet, P., & Frith, C. (2002). Neural correlates of perceptual learning: A functional MRI study of visual texture discrimination. *Proceedings of the National Academy of Science of the USA, 99*, 17137–17142.

Snowden, R. J. (1992). Orientation bandwidth: The effect of spatial and temporal frequency. *Vision Research, 32*, 1965–1974.

Sowden, P. T., Rose, D., & Davies, I. R. L. (2002). Perceptual learning of luminance contrast detection: Specific for spatial frequency and retinal location but not orientation. *Vision Research, 42*, 1249–1258.

Tanaka, K., & Fujita, I. (1991). Coding visual images of objects in the infero-temporal cortex of the macaque monkey. *Journal of Neurophysiology, 66*, 170–189.

Vaina, L. M., Belliveau, J. M., Burin de Roziers, E. B., & Zeffiro, T. (1997). The relationship between cortical activation and psychophysical performance in humans during fast learning of motion discrimination. *Neuroimage, 5*, 137.

Vidyasagar, T. R., & Sigüenza, J. A. (1985). Relationship between orientation tuning and spatial frequency in neurones of cat area 17. *Experimental Brain Research, 57*, 628–631.

Vogels, R., & Orban, G. A. (1994a). Does practice in orientation discrimination lead to changes in the response properties of macaque Inferior temporal neurons? *European Journal of Neuroscience, 6*, 1680–1690.

Vogels, R., & Orban, G. A. (1994b). Activity of inferior temporal neurons during orientation discrimination with successively presented gratings. *Journal of Neurophysiology, 71*, 1428–1451.

Westheimer, G., Shimamura, K., & McKee, S. P. (1976). Interference with line-orientation sensitivity. *Journal of Optical Society of America, 66*, 332–338.

Yang, T., & Maunsell, J. H. R. (2004). The effect of perceptual learning on neuronal responses in monkey visual area V4. *Journal of Neuroscience, 24*, 1617–1626.

Zohary, E., Celebrini, S., Britten, K. H., & Newsome, W. T. (1994). Neuronal plasticity that underlies improvement in perceptual performance. *Science, 263*, 1289–1292.